Food Gathering Behavior of the Ant, *Camponotus noveboracensis* (Fitch) (Hymenoptera: Formicidae)[1]

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Abstract: A study of the food gathering behavior of a single colony of *Camponotus noveboracensis* (Fitch) revealed that its food sources, during the period studied, were the honeydew produced by the membracid, *Vanduzea arquata* (Say), the sap exudate flowing from a wound in the trunk of a common lilac, *Syringa vulgaris*, and the carcasses of dead insects. The behavior of the worker ants in exploiting each of these sources is discussed in detail.

INTRODUCTION

Camponotus noveboracensis (Fitch) is a nearctic ant that can be found from coast to coast across North America, mainly at latitudes between 40° and 48° N (Creighton, 1950). While similar in appearance to *C. herculeanus*, *C. noveboracensis* was recognized as distinct from the former species by Creighton in 1950. Indeed, this ant has a confusing taxonomic history, beginning in 1879 when Forel overlooked Fitch's original description and redescribed the ant as *C. herculeanus* subsp. *ligniperda* var. *pictus*. *C. noveboracensis* has a dark red thorax and petiole and a black head and gaster and can be distinguished from *C. herculeanus* by, among other things, its relatively longer antennal scapes (see Creighton, 1950, for a detailed discussion of the differences between these species). While elements of the biology of *C. noveboracensis* have been discussed by Talbot (1934, 1965), Gregg (1944, 1963), Kannowski (1959), and Sanders (1964), little information has appeared on its feeding behavior. Sanders (1964) did discuss its food sources briefly, and Jones (1929) listed aphid species from which *C. noveboracensis* gathers honeydew excretion. Also, Buckingham (1911) recorded a series of observations on foraging and trophallaxis by this species (as *C. herculeanus pictus*).

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The present investigation provides data on the food gathering behavior of a single colony of *C. noveboracensis.* This colony was observed to have three food sources: (1) the honeydew excretion of the membracid, *Vanduzea arquata* (Say); (2) the sap exudate from a wound in the bark of a common lilac, *Syringa vulgaris*; and (3) the carcasses of dead insects. Each of these sources is discussed in detail.

METHODS

The observational portion of this investigation was carried out in the fall of 1967 from 4 September to 12 November. Observations were made daily and included meteorological data. Regular counts were made of both ants and membracids, and a series of the ants was dissected in the laboratory in order to examine and measure their crops. Head measurements of these ants were made following the method defined by Wilson (1964).

RESULTS AND DISCUSSION

Description of Ant Colony.

The colony investigated was located beneath and probably within the framework of a house in a residential district of Ithaca, New York. While *C. noveboracensis* has been reported from a great variety of habitats, this particular location is somewhat unusual. There are no reports in the literature examined of this ant being a house pest, although closely related species, *C. pennsylvanicus* (DeGeer) and *C. ferrugineus* (Fabricius), do invade such wooden structures (Smith, 1965). *C. noveboracensis* is most often found in "dead wood of standing or prostrate trunks" (W. M. Wheeler, 1910), and has been reported to invade live trees of balsam fir, *Abies balsamea* (L.) (Sanders, 1964). In addition, colonies have been found in the soil alone (Talbot, 1965) and have been twice taken on the grasslands of North Dakota in cow dung (G. C. Wheeler, 1963). This ant has been reported from boreal forests (Sanders, 1964), swamps and marshes (Talbot, 1965), tamarack bogs, fields, forest margins, oak forest, beech-maple forest (Gregg, 1944), pine dunes and black oak forest on sand (Talbot, 1934), aspen forest, ponderosa pine forest, Rocky Mountain Birch grove (Gregg, 1963), pioneer dunes and along the rocky shore of Lake Superior (Gregg, 1946).

Only two foraging trails were observed coming from the colony under study. Both of these trails were permanent and both issued from the same opening beneath a concrete sidewalk adjacent to the house. One trail led to a series of membracid aggregations and the other, running more or less perpendicular to the former, led to a lilac bush. Other foraging trails were searched for but none were found. It is certainly possible that these ants were also foraging beneath the house for various arthropods. A number of individuals would occasionally stray from the trail leading to the lilac and appeared to be engaged in general foraging. This straying behavior is similar to the trail "leakage" phenomenon discussed by Holt (1955) for *Formica rufa* and may account for the discovery of insect carcasses which are carried back to the nest. When the ants' foraging activities finally ceased (30 October) an unsuccessful attempt was made to reach the colony's actual location.

Ant-membracid Commensalism.

The aggregations of the attended membracid, *Vanduzea arquata* (Say), were located on a small common locust tree, *Robinia pseudoacacia* L. This tree was 1.73 m. high and of two parts, each entering the ground separately, but most likely sharing the same root system. The circumference, at ground level, of the main trunk was 5.08 cm. and that of the secondary trunk was 2.54 cm. A Taylor maximum-minimum self-registering thermometer was suspended from the main trunk at a height of 100 cm.

V. arquata is sexually dimorphic and easily sexed in the field. The females are brown with yellowish white markings, while the smaller males are dark brown (almost black) with small whitish markings. This membracid is widely distributed throughout the United States and is abundant in the Cayuga Lake basin. Its biology has been reported on in detail by Funkhouser (1915, 1917) who has described it as being "decidedly gregarious" (1915). Males, females, and nymphs of various instars aggregate into small clusters, usually at the bases of branches. Oviposition occurs at three distinct times during the year: the middle of June, the end of July and in September (Funkhouser, 1915). Funkhouser (1915) reports the following ants attending *V. arquata* in the Ithaca area: *Formica obscuriventris* Mayr, *Formica exsectoides* Forel, *Camponotus pennsylvanicus* (De Geer), *Crematogaster lineolata* (Say), *Prenolepis imparis* (Say).

Because the membracids aggregate at more or less permanent locations, these sites can be permanently tagged and observed. Four clusters were recognized at first, three on the main trunk or its branches at heights of 69 cm., 81 cm., and 124 cm. from the ground and one on the secondary trunk at a height of 76 cm. Individual strays and small clusters of two or three individuals were common but not permanent in location. Three additional clusters were discovered on 4 October. None of these had existed previously. Strays of both membracids and ants were occasionally counted in order to assess the total number of individuals on the tree. Group counts were begun on 9 September and were ended on 10 November and were made approximately every two days.

Figure 1 (the reader is cautioned that the scale of the abscissa is not linear, i.e. equal distances along the abscissa do not represent equal numbers of days) graphs the total numbers of *C. noveboracensis* workers and *V. arquata* males, females, and nymphs counted in the four tagged aggregations at each observation. The number of attending ants is strongly correlated with the number of membracids in each aggregation with a correlation coefficient of .973. This

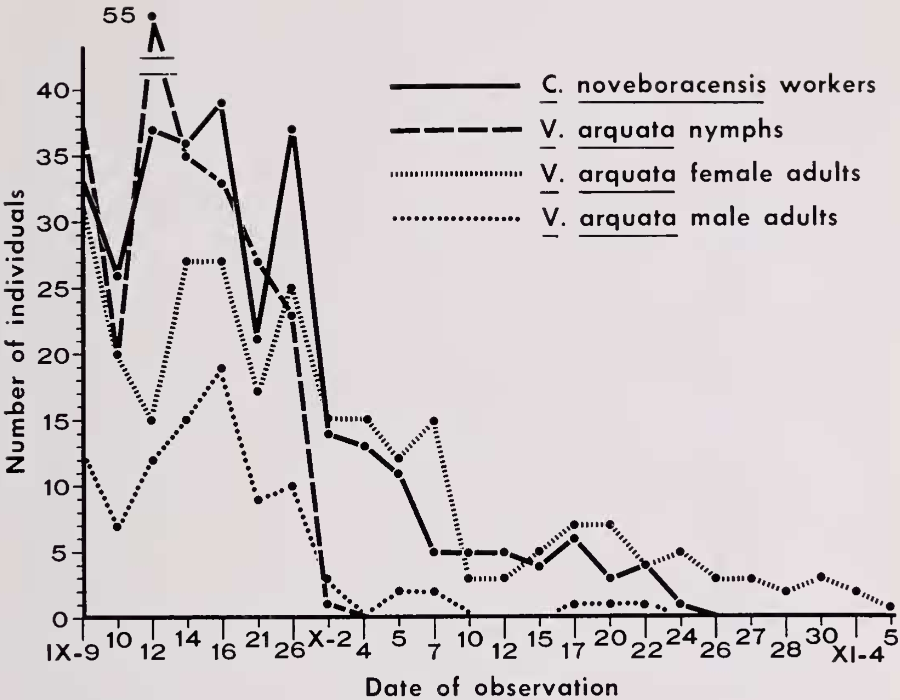
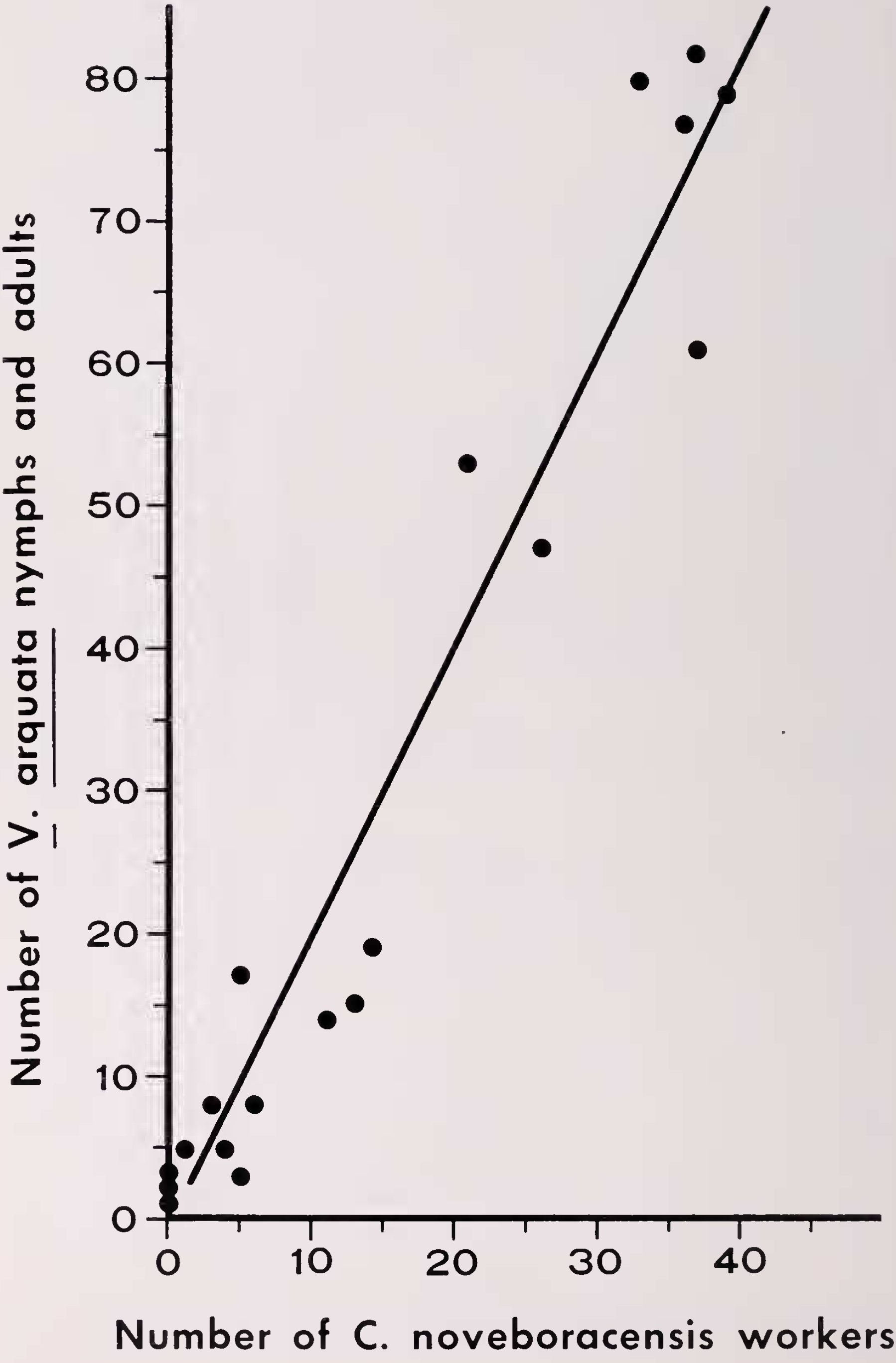


FIG. 1. Total numbers of *C. noveboracensis* workers and *V. arquata* males, females, and nymphs counted in four tagged aggregations. Roman numerals on abscissa indicate the month (the scale of the abscissa is irregular).

correlation is further illustrated by the scatter diagram and regression line in Figure 2. Evidence of this correlation was also seen in other counts made of three additional clusters and in counts made of strays. Andrews (1929), in his investigation of the relationship between *V. arquata* and *Formica exsectoides*, found "no fixed relationship of number between" these two species nor did he report any linear relationship at all between numbers of ants and membracids found together.

As the fall season progressed the total numbers of individuals steadily decreased (Fig. 1). For the ants and female membracids this decrease began after 26 September, for the male membracids after 16 September and for the membracid nymphs after 12 September. On 4 October three other clusters were found, and the formation of these clusters probably accounted for the initial decline in numbers at the original sites, at least for ants and female membracids. On 26 September there were 37 ants and 28 female membracids present in the original four aggregations. On 4 October there were 13 ants and 15 female membracids at these locations, while on that same date in the three new aggregations there were 13 ants and 16 female membracids. The totals of these figures


Number of V. arquata nymphs and adults
0
10
20
30
40
50
60
70
80
0
10
20
30
40
Number of C. noveboracensis workers

for 4 October are close to the totals for 26 September. In each case these figures do not take into account individual strays. The formation of the new clusters cannot account for the changes in numbers of membracid males or nymphs. The total number of males in the original four groups went from 19 individuals on 6 September to 0 on 4 October, while in the three newly formed aggregations, only one male was seen. Between 12 September and 4 October the number of nymphs in the original aggregations went from 55 to 0 individuals. No nymphs were ever seen in the newly formed aggregations, although one was found as a stray on 7 October.

The increases and decreases in numbers of membracid individuals in the groups examined would indicate that they are quite mobile, although Funkhouser (1915) stated that they remained at one location for long periods of time. The males seem especially mobile. They were seen to fly away from and arrive at the locust tree quite regularly. They also appeared more active within the aggregations. The adults are quite prone to hop off the tree if abruptly disturbed by touch or by rapid movement of the branches. This is also recorded by Andrews (1929) and Funkhouser (1915).

The fluctuations in numbers of nymphs are difficult to explain. The nymphs are cryptically colored, and all instars (a total of 5), thus including the very small, can be found within a single aggregation. Both of these factors can lead to counting errors. But the sharp increase from 20 individuals on 10 September to 55 on 12 September is probably not due to counting error. Since the nymphs were never counted on the basis of instar, this addition of 35 individuals may have been from a newly hatched brood, although this does not seem to fit Funkhouser's (1915) oviposition schedule. Even more difficult to explain is the sudden decrease of nymphs from 55 individuals on 12 September to 0 on 4 October. It would not appear from examing adult counts that these nymphs were maturing and moulting into adults, unless these adults migrated immediately. Nor would it seem probable that the nymphs themselves were moving off the tree. The nymphs are far more sedentary and gregarious than the adults. It should be noted that because of these nymphal characteristics, very few stray nymphs were ever found and the counts in the original four aggregations probably are a good estimate of total number of nymphs on the tree. Predation by membracid enemies or by the attendant ants may account for this sudden drop in numbers of nymphs, but such predation was never observed. Andrews (1929) reported that dead or severely injured *V. arquata* individuals are carried off as food by the attendant ant *Formica exsectoides*.

Never at any one point in time did the number of male membracids total more

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Fig. 2. Relationship of total numbers of *C. noveboracensis* workers to total numbers of *V. arquata* nymphs and adults in four tagged aggregations.

than the females (Fig. 1). This is true for the original four aggregations, the three newly formed aggregations and for the smaller groups and strays. This is in direct contradiction to Funkhouser's (1915) observations. He reported that in the fall the males are more numerous than the females, and he regularly observed a ratio of five to one.

During this investigation the temperature ranged from 30°C to –4°C. The last nymph was recorded on 10 October, the last male on 22 October, the last female on 10 November and the last *C. noveboracensis* worker on 28 October. One light snowfall occurred on 8 November. Funkhouser (1915) reported *V. arquata* present to late October.

On 26 October two specimens of the ant *Prenolepis imparis* (Say) were observed on the main trunk of the locust tree. There were only three specimens of *C. noveboracensis* present. Although *P. imparis* was observed foraging on the ground around the locust tree during the entire investigation, it was never seen on the locust while *C. noveboracensis* was present in large numbers. As many as 14 *P. imparis* were observed (28 October) attending the membracids. The last *P. imparis* was seen on 10 November. This increase in activity on the part of *P. imparis* not only corresponds to the decrease in numbers of *C. noveboracensis*, but also to a general lowering in the daily air temperature. Talbot (1943) described *P. imparis* as a cold weather ant and found that this ant reaches its peak of foraging activities at temperatures between 45° and 60°F. At the time 14 *P. imparis* workers were counted, the air temperature was 42°F.

In collecting honeydew from homopterans, ants have been most generally described as stimulating the individual homopterans with stroking movements of their antennae. Wheeler (1910) speaks of this stroking behavior as antennal caresses, and both Funkhouser (1915) and Andrews (1930) described this in particular for ants attending *V. arquata*. Andrews (1930) described in detail the honeydew reflexes of *V. arquata* and the soliciting behavior of *Formica fusca* L. *V. arquata* nymphs produce droplets of honeydew by extending and raising the tip of their abdomen. The adults raise the tip of their abdomen but also rise up on their legs, inclining themselves anteriorly downward. These droplets are produced regardless of whether there are ants in attendance or not. Andrews (1930) reported that honeydew is produced without a detectable external stimulus, although the nymphs can be induced to produce droplets by touching them with forceps, various brushes, or amputated ant antennae. Attendant ants actually touch the membracids with their antennae and palpi. *C. noveboracensis* was observed in this investigation to move rapidly over the membracids touching them or just waving over them with their antennae and palpi. The antennae are generally waved up and down alternately. Andrews (1930) found no indication that *F. fusca* stimulated *V. arquata* to produce honeydew droplets in any precise way, and a similar conclusion was reached in this investigation for *C. noveboracensis*. Droplets are produced by the membracids even in the absence of ants, but the stroking by the ants might conceivably increase the rate of droplet formation.

Both Funkhouser (1915) and Andrews (1930) reported that the nymphs produced more droplets than the adults, and Andrews recorded a female giving a total of 10 drops to attendant ants (*F. fusca*) in a period of 42 minutes. He also recorded one nymph giving 5 drops in 46 minutes, another 4 drops in 50 minutes, and another 5 drops in 35 minutes. His data do not support his conclusion that the nymphs produced droplets more often. The male was not recorded.

The present investigation found the following droplet production rates: on 16 September (24°C) a nymph was found to produce 39 droplets in 23 minutes, with an average time interval between droplets of 36 sec.; the shortest interval was 1 sec. and the longest 3 min. 18 sec.; an adult female was found to produce 35 droplets in 24 minutes with an average time interval between droplets of 43 sec.; the shortest interval was 9 sec. and the longest 1 min. 55 sec.; and on 20 September (26°C) a nymph was found to produce 36 droplets in 19 minutes with an average time interval between droplets of 33 sec.; the shortest interval was 1 sec. and the longest 2 min. 50 sec.; an adult female was found to produce 36 droplets in 25 minutes with an average time interval between droplets of 50 sec., the shortest interval was 15 sec. and the longest 2 min. 34 sec. These figures indicate that the nymphs are producing more droplets than the adult females at the temperatures indicated. But they also suggest that the ants are receiving much more honeydew from the female adult than was indicated by Andrews (1939, 1930) and Funkhouser (1915). Andrews did not mention male droplet production, and it should be noted that in this investigation the males were never observed to give droplets of honeydew to the workers of *C. noveboracensis*. Within the aggregations the males were moving about often, crawling over the more sessile females and were quite easily disturbed. It would appear that the honeydew gathered by the ants comes almost exclusively from the nymphs and female adults. Andrews (1929) noted that the droplets formed by the adults (no reference to sex) were often smeared between the tips of the wings, but this phenomenon was never observed in this study.

Besides actually soliciting and gathering honeydew, three other behavior patterns were noted for the ant workers on the tree. One was a "searching" pattern, in which workers ran out on leaves and leaflets near membracid aggregations, and the others were self-grooming and food transmission or trophallaxis. Both self-grooming and trophallaxis were prevalent in the activities surrounding the membracids. Regurgitative feeding and crop storage are important social functions in the biology of ants (Eisner, 1957), and once food is returned to the nest, food transmission can occur at a rapid rate within the colony (Wilson and Eisner, 1957). All workers on the locust tree appeared to participate in food transmission and all seemed to collect honeydew. Buckingham (1911) observed trophallaxis in this ant and concluded that no single size group of individuals could be the sole regurgitators. All sizes of the workers were involved in food transmission (though Buckingham willingly admitted that the direction of transmission was difficult to determine), although the larger workers did more soliciting for and receiving of food because they did less collecting.

A total of 28 workers returning to the nest from the membracid aggregations captured at random over a period of 14 days (from 11 to 24 September) were dissected in order to examine their crops. Over the same period of time 22 workers going from the nest to the membracids were collected and dissected. The head length and width for each of these workers was measured and the cephalic index ($HW / HL \times 100$) was computed for each. The crops and gasters were arbitrarily classified as belonging to one of four conditions: crop empty, crop partially full, crop full but gaster not distended, and crop full with gaster distended (the crop could be observed only by carefully removing the tergites and sternites of the third and fourth abdominal segments; in lateral view the crop was then measured across its widest point perpendicular to the longitudinal axis of the ant). In the latter two cases the viscera were pushed back by the full crop into the last two visible segments of the gaster. When the gaster was distended the tergites were pulled from one another, as were the sternites, stretching the intersegmental membranes and giving the gaster a translucent quality. The workers going to and from the membracids had a mean head length of 1.67 mm., a mean head width of 1.54 mm., and a mean cephalic index of 91. The significance of these figures will be apparent when they are later compared with those of the ants gathering sap exudate. The mean crop width of those workers going to the membracid aggregations was 0.51 mm., while that of the returning workers was 1.50 mm. Of the 22 workers going to the membracids, five had crops which were partially full, the remaining workers had empty crops. Of those workers returning to the nest, one had an empty crop, four had partially full crops, ten had full crops without the gasters being distended, and thirteen had full crops and distended gasters. Five of the ants returning to the nest were collected at 2300 hours (Eastern Standard Time) on 26 September, and four of the five had full crops. As will be pointed out later, ant activity slows at night, but the collection of honeydew probably continues at a slow rate. Although it would appear that all workers are collecting honeydew, some return to the nest with their crops only partially full. Though this may or may not indicate a partial division in labor in collecting honeydew, it gives no indication of what may be the stimulus for returning to the nest.

Several factors—light, temperature, wind velocity and precipitation—play a role in governing the honeydew soliciting and collecting activities of the ants, either directly, or indirectly by affecting membracid behavior. The individual effects of each of these factors cannot be clearly defined. It is particularly difficult to separate the affects of temperature and light, although it was generally observed that ant and membracid activity decreased at night and with lower temperatures. *C. noveboracensis* attended *V. arquata* 24 hours a day. At night and in conjunction with lower temperatures, the membracids and ants became lethargic and often remained motionless for long periods of time. Andrews (1929) reported also that *Formica exsectoides* attended *V. arquata* overnight and that some ants moved back and forth to the nest. While it is clear that in the fall *C. noveboracensis* is primarily diurnal in its foraging habits, other species of *Camponotus* reach the peak of their foraging behavior at night. Pricer (1908) reported that *C. pennsylvanicus*, a closely related species to *C. noveboracensis*, is most active at night in gathering honeydew from aphids, and Gupta (1963) found that the common black ant of India, *C. compressus* (Fabricius), is negatively phototropic and reaches the peak of its foraging activity at 4 o'clock in the morning. This latter ant, however, is most likely avoiding the intense heat of the tropical day.

Rain was found to inhibit the activities of both *C. noveboracensis* and *V. arquata*. During rain both the membracids and the ants migrated to the undersides of the branches (*V. arquata* is normally found on the upper surfaces). The ants remain still, and no honeydew is collected. Andrews (1929) found a similar reaction on the part of *F. exsectoides* to rain but made no reference to the membracids. Wind was also observed to inhibit activity. Neither the membracids nor the ants could move about easily in strong wind, and both were observed to be blown from the tree under such conditions. Gupta (1963) recorded a similar drop in activity for *C. compressus* during times of increased wind velocity.

The flow of individual worker ants, either to or from the nest, past a particular census point was used as an index to the level of their activity while collecting honeydew. These observations were made during 30 minute units with the air temperature being recorded at the end of each unit. The time interval between each ant (traveling in the same direction) was recorded. The ant trail leading to and from the locust tree was 6 meters long from the point of exit to the bases of the tree. Half of the trail was generally exposed and on the surface of the sidewalk. The other half ran, only semi-exposed, through thick grasses. The flow census point was marked at about midway along the trail. The time that it took to travel the trail distance of 6 meters was recorded for four workers going to the locust tree and four workers returning to the nest. For those going to the tree, the times were 5 min. 18 sec., 6 min. 28 sec., 5 min. 36 sec., and 7 min. 17 sec. for a mean time of 6 min. 10 sec. For workers returning to the nest, the times were 5 min. 35 sec., 5 min. 33 sec., 6 min. 00 sec., and 6 min. 07 sec. for a mean time of 5 min. 49 sec. Workers of *C. noveboracensis* occasionally strayed from the trail and did not follow it with great facility. This was particularly true after rain, when many individuals apparently experienced great difficulty staying on the trail at all. This may indicate that this ant relies heavily on chemical cues in trail following. Workers were occasionally observed removing small stones from the trail.

The peak rates of flow corresponded well with the peaks in population density within the four original ant-membracid aggregations (Fig. 1). These corresponding peaks occurred on 9 September, 12 to 16 September, and 26 September. The flow of workers was never greater than 1.06 per minute, and this occurred at the highest temperature recorded in any of the observational units. Andrews (1929) made some trail counts of *F. exsectoides* going to and from *V. arquata* aggregations, but for several reasons (different time of year, lack of recorded temperatures and time of day information, etc.) his figures cannot be compared to those recorded in this investigation.

Wasps of the genus *Vespula* were frequently seen flying near the ant-membracid aggregations and perhaps were attracted by honeydew deposits on the leaves of the locust tree. None of these wasps was ever seen to land on the tree, although one did touch a branch near one aggregation. The ants became excited but did not attack the wasp, and it quickly flew away. One wasp was held with forceps near an aggregation, and it was attacked by several ants, all of whom made attempts to bite it. Two individual wasps were collected at different times and were identified as *Vespula maculifrons* (Buysson).

The literature on ant-homopteran commensalism is vast. Recent reviews of this relationship have been published by Way (1963) and Sudd (1967). The most intriguing questions arising from studies of this relationship are those concerning the benefits derived by the homopterans and those concerning the evolution of such commensalism. The membracids themselves, when in association with ants, have been examined in less detail than the aphids and coccids, and much remains to be discovered about their role in this relationship.

Gathering of Sap Exudate.

The literature abounds with accounts of ants directly gathering plant sap or juices. These plant liquids may be collected from floral or extrafloral nectaries (Wheeler, 1910) or by biting the stems of succulent plants and collecting the resultant cell sap exudate (Ayre, 1959). Also, ants may gather sap flowing from plant wounds. For example, *Formica rufa* has been observed gathering sap running from the ends of broken birch twigs (Elton, 1932). Such ant and plant liquid relationships can be obligatory or facultative. While there are dramatic examples of obligatory mutualism, for example the relationship between ants of the genus *Pseudomyrmex* and the swollen-thorn acacias, in which, among other things, the ant gathers sweet fluids from foliar nectaries (Janzen, 1966), most of such relationships appear to be facultative. It might be convenient to regard facultative relationships as being either cyclically habitual or opportunistic. A cyclically habitual relationship may be defined as occurring when an ant colony gathers plant liquids at a particular season each year from the same or similar sources as dictated by its habitat. For example, in the spring, all the liquid foods of *Formica subnitens* appear to be obtained from the exudates of the young shoots and buds of *Pinus ponderosa* Laws (in the case studied) (Ayre, 1959). The collecting of sap from plant wounds is described here as being opportunistic. While plant liquids, other than honeydew, may not comprise a very large part of any ant colony's diet (estimated by Sudd, 1965, to be 4.5% for the wood ant, *Formica rufa*), they appear to be of greater importance in the spring of the year than at any other time.

The second of the two foraging trails issuing from the colony of *C. noveboracensis* was discovered on 16 September. It led, in a meandering fashion, to a wound in the trunk of a common lilac, *Syringa vulgaris,* from which the ants were collecting sap. The shortest distance from the trail's point of exit to the base of the lilac was approximately 3.8 meters. About one-fourth of its length was completely concealed beneath a loose assortment of stones and broken pieces of concrete. Most of the remainder of the trail was only semi-exposed as it ran through thick grasses. The lilac was estimated to be about 3 meters high, and the circumference of the trunk at ground level was 12.7 cm. Although the wound in the bark of the tree was about 5 cm. long and ran parallel to the trunk, the sap oozed from only a small area of the wound at its lower margin. This area was 7.6 cm. up the trunk from the ground.

The worker ants gathered in a circle about that portion of the wound from which the sap was issuing, each with its head projecting over the edge of the margin, imbibing the sap. While trophallaxis was an integral part of the overall behavior pattern in gathering honeydew, it was not in gathering sap. Regurgative exchange of food between individual workers was observed only once on the lilac. The ants appeared to come to the wound, imbibe the sap and then return to the nest. There were two exceptions to this general pattern: individuals sometimes appeared to forage in general on the lilac trunk (none were ever seen carrying any prey), and they sometimes appeared to be "defensively" poised near the wound.

Counts of workers collecting sap were made two to seven times each day (when counts were made) for a period of more than two weeks. These counts were made at various times of the day and were aimed at determining the colony's pattern of activity with respect to gathering the sap. The ants were active in this capacity 24 hours a day. The results of the counts are graphed in Figure 3, and two generalizations regarding the graph are possible. Firstly, most population peaks occurred between 1900 and 0100 hours, and most lows

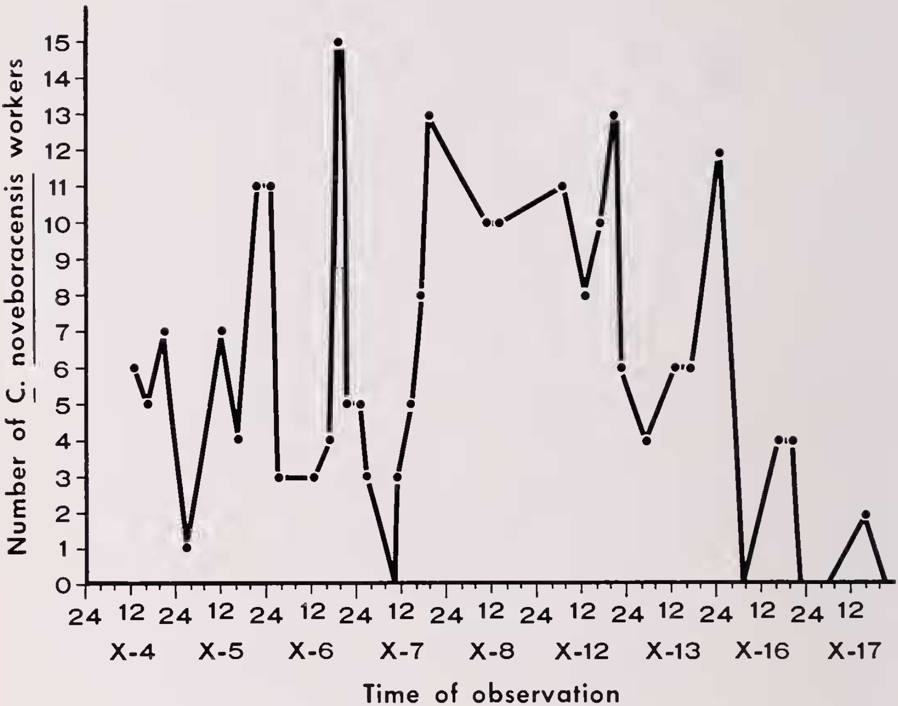
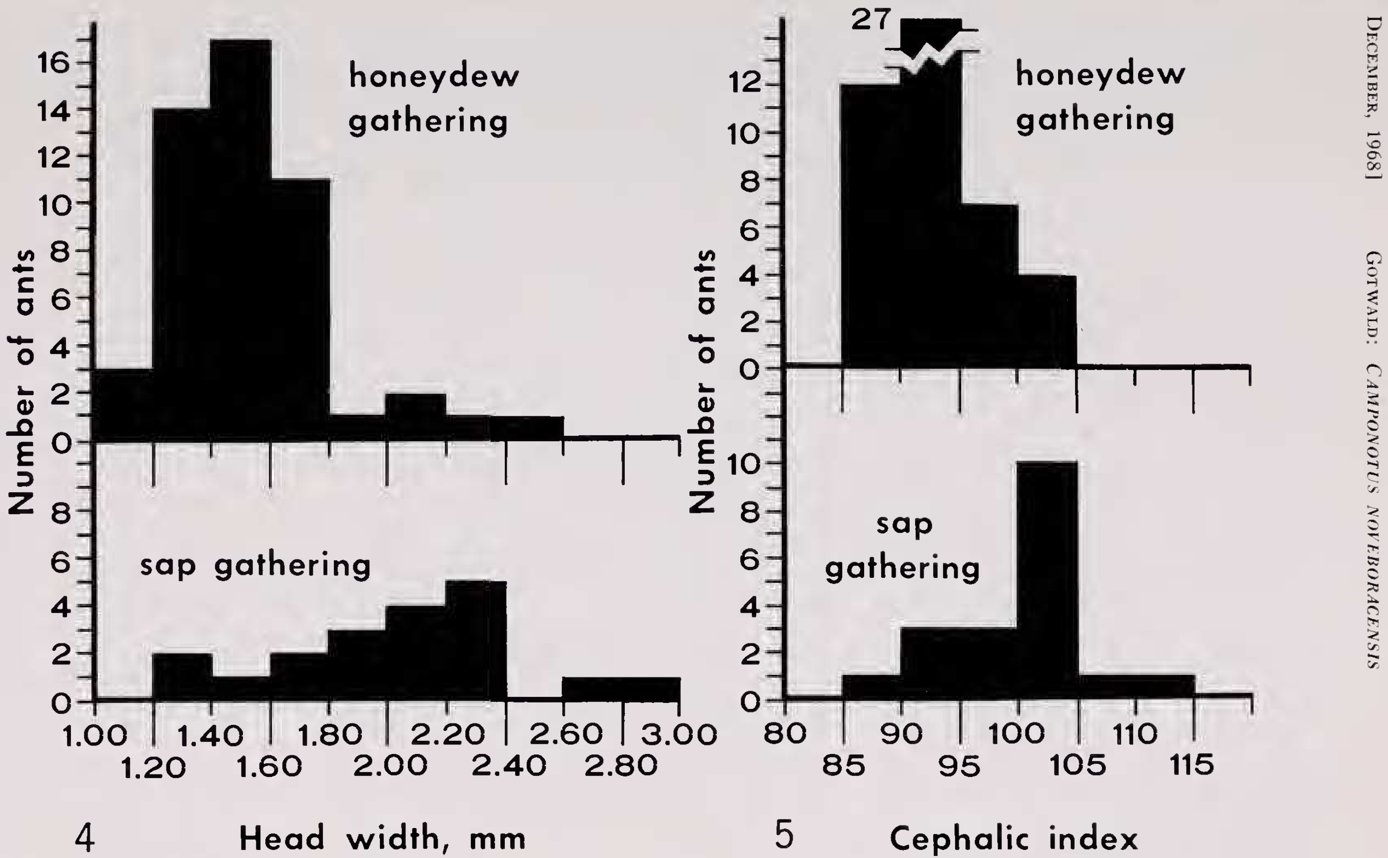


Fig. 3. Daily pattern of sap-gathering activity for workers of *C. noveboracensis*. Upper row of numerals on the abscissa indicates the hour (Eastern Standard Time); lower row indicates the month and day.

occurred around 0800 hours. The second and less substantial generalization is that the overall curve formed during this time period is approximately bell-shaped with most sap collecting activity occurring between 5 and 16 October. Thus the daily activity pattern is different from that involved in gathering honeydew. It is, in essence, crepuscular and nocturnal, while that of honeydew gathering is primarily diurnal. This daily activity pattern may be a reflection of maximum sap flow since, in the vascular plants, the photosynthetically produced sugars are generally stored in the leaves as insoluble starches immediately after being produced during the daylight hours and are translocated down the phloem as sugars at night. The shape of the curve formed over the time period of observations suggests that the sap gathering may have begun only several days prior to the initial observations.

As was the case with honeydew deposits, wasps of the genus *Vespula* were often seen flying about the wound in the lilac. One wasp was seen to land near and inspect the wound. The three ants that were present did not react aggressively toward the wasp. They did, however, remain stiffly poised with



FIGS. 4–5. Frequency distributions of head widths and cephalic indices of *C. noveboracensis* workers gathering honeydew and gathering sap.

their antennae pointed at the wasp. The wasp was aggressive and made several quick moves toward the ants. This wasp was eventually collected and identified as *Vespula maculifrons* (Buysson).

A total of 12 workers returning to the nest from the lilac, and 7 going to the lilac from the nest, were collected at random over a period of 19 days (from 16 September to 4 October) and were dissected in order to examine their crops. The head length and width of each of these workers was measured and the cephalic index was computed for each. The crops and gasters were found to be in any one of the four conditions previously described for the honeydew gathering workers. The workers going to and from the lilac had a mean head length of 2.03 mm., a mean head width of 2.04 mm., and a mean cephalic index of 100. The mean crop width of those workers going to the lilac was 0.54 mm. while that of the returning workers was 1.72 mm. All of the 7 workers going to the lilac had empty crops. Of the 12 returning workers, one had an empty crop, two had partially full crops, six had full crops without the gasters being distended, and three had full crops and distended gasters.

While observing both honeydew and sap gathering activities, it was noted that the workers gathering sap appeared to be larger than those gathering honeydew. The frequency distributions of head widths of both groups of foragers are compared in Figure 4, and the frequency distributions of cephalic indices are seen in Figure 5. Using Student's t test, the head widths of the sap gathering group were found to be significantly larger at the 1% level than those of the honeydew gathering group. A statistical analysis of the cephalic indices, using Wilcoxon's two sample test (Steel and Torrie, 1960), revealed that the indices of these two groups are significantly different also at the 1% level. On the basis of head size and head shape then, it is evident that two different portions of the colony were engaged in the two different foraging tasks.

Studies on the genus *Camponotus* have revealed that the workers of particular species may form a continuous and gradual series from the smallest to the largest or that they may be distinctly bimodal in size distribution. Smith (1942b) found, when plotting head widths against number of individuals in a colony, that *C. noveboracensis* forms a gradual series so that the "classes" of workers are not clearly defined. He also found that the curve formed was distinctly skewed to the left, indicating that minor workers comprise the largest number of individuals in the colony. Buckingham (1911) found similar results for *C. noveboracensis*. For other species Smith (1942b) found that *C. pennsylvanicus* was not completely gradual in distribution but neither was it distinctly bimodal, that *C. santosi* Forel and *C. planatus* Roger were bimodal with connecting media workers, and that *C. inaequalis* Roger was bimodal with no intermediates between the groups. Sanders (1964) found for *C. herculeanus*, in plotting head width against numbers of ants, that a biomodal curve resulted. Buckingham (1911) calculated that the workers of *C.*

americanus formed a continuous, gradual series, and Pricer (1908), using worker body length, reported a gradual series for *C. pennsylvanicus* and *C. ferrugineus*. Wilson (1953) described *Camponotus abdominalis floridanus* (Buckley) as exhibiting partial dimorphism and argued that worker polymorphism should not be defined in terms of frequency, since many truly polymorphic species are apparently unimodal. Buckingham and Pricer both attempted to link worker size differences to specialized work tasks. Buckingham provided little information on foraging, but Pricer found, for *C. pennyslvanicus*, that smaller workers gathered honeydew from aphids. This honeydew was passed on, at the base of the tree where the aphids were located, to the next largest size group which in its turn carried the honeydew to the nest. Pricer indicated that the smallest and largest workers were "house-keepers." Thus it is even clearer that for *C. noveboracensis*, which forms a gradual polymorphic series, there is a foraging specialization on the part of the workers, either based on or coincidental with a difference in size.

Little information could be found in the literature on *Camponotus* plant-juice gathering activities, although it seems to be generally acknowledged that plant juices do form a definite part of the diets of most formicine ants. Pricer (1908) reported that *C. pennsylvanicus* extracted juice from a large stalk of "pie-plant," and Ayyar (1935) observed *C. compressus* to "abstract" vegetable juices from tender shoots, flowers and "sacchariferous" glands.

Gathering Carcasses of Dead Insects.

Workers were often seen foraging in the vicinity of the trail leading to the lilac bush. It was previously suggested that this foraging activity was the result of trail leakage, i.e. workers occasionally or perhaps predictably straying from the trail. Trail leakage would appear to provide these ants with the opportunity of discovering and utilizing new food sources. The area covered by these foragers encompassed approximately 2 square meters. Two workers returning from this area were found carrying the carcasses of dead insects. One was carrying an adult fly of the family Calliphoridae and the other a homopteran adult of the family Fulgoridae.

Workers were also observed returning to the nest with insect carcasses on the trail leading to the membracid aggregations. One was found with the desiccated carcass of a lepidopterous larva and another with the head of a wasp. In the latter case, after a thorough search of the trail, the remainder of the wasp was recovered and identified as *Vespula vulgaris* (L.). The worker ant carrying the wasp head was collected and dissected. Its crop was partially filled with honeydew indicating that it may have been returning from the locust tree when it discovered the dead wasp.

From these observations it is difficult to assess the relative importance of predation versus scavenging as a source of whole proteins in the diet of *C.*

noveboracensis. Sanders (1964) reported one worker of this species carrying a dead spruce budworm larva, *Choristoneura fumiferana* (Clem.), and Green and Sullivan (1950) observed ants which they identified as *Camponotus herculeanus ligniperdus* attacking larvae of the forest tent caterpillar, *Malacosoma disstria* Hbn. In this latter case it can be assumed that they were observing *C. noveboracensis*, since the varietal name was not cited (the name they used is that of a European species). They reported that this ant and *Formica fusca* attacked and carried back to their nests the first to fourth instar larvae. Two types of attacks were noted for both species, one as the result of foraging and the other as the result of attending workers being disturbed when caterpillars crawled among the aphid groups from which the workers were gathering honeydew.

Beyond this, at best, only inferences can be drawn about *C. noveboracensis* and its predation and scavenging habits from observations of the feeding habits of closely related species. Pricer (1908) reported that he had never seen either *C. pennsylvanicus* or *herculeanus* take insects alive, but that they often sucked the "juices" from dead insect carcasses, sometimes carrying the heads of the dead and consumed insects back to the nest. Smith (1942a) reported from laboratory experiments that cannibalism of *C. pennsylvanicus* larvae by attending nurse workers increased when the colony's food supply was reduced. Sanders (1964) observed *C. herculeanus* workers carrying a mosquito and a beetle (Lampyridae) to their nest, and Ayre (1963a) described, from laboratory experiments, the feeding of *C. herculeanus* on housefly larvae, and further reported (1963b) that this species was an effective predator.

CONCLUSIONS

Based on observations made of a single colony of *Camponotus noveboracensis,* the following conclusions are offered regarding the food gathering behavior of this species during the fall season:

1. The major sources of food for the colony are plant liquids, either in the form of homopteran produced honeydew (in this case from the membracid, *Vanduzea arquata*) or sap exudate. This diet is supplemented with proteinaceous materials from the carcasses of dead insects.

2. The number of worker ants gathering honeydew is strongly correlated with the total number of membracids present.

3. Female adults and nymphs of *V. arquata* are *both* an important source of honeydew for the colony, while the males appear unimportant in this respect.

4. Although the number of *C. noveboracensis* workers is correlated with the number of membracids, the ants abandon their honeydew food source prior to the disappearance of the membracids. In the case investigated, the ant *Prenolepis imparis* took the place of *C. noveboracensis* and continued to collect the honeydew.

5. While the benefits of the ant-homopteran commensalism for the ants are obvious, those for the membracid *V. arquata* are not. For each organism, the relationship does not appear to be obligatory.

6. Trophallaxis occurs at different rates between workers gathering honeydew, where food transmission is frequent, and those gathering sap, where it is infrequent.

7. The gathering of honeydew for this ant, in terms of peak rates of activity, follows a diurnal pattern, whereas the collecting of sap is crepuscular and nocturnal.

8. The rate of collection of honeydew by the workers is slowed by lower temperatures, increased wind velocity, and precipitation.

9. Workers collecting sap are significantly larger than those collecting honeydew; thus two different polymorphic segments of the colony may be specialized for two different foraging tasks.

10. While it may be suspected that workers collected some proteinaceous food by predation on other insects, this investigation indicates that most proteinaceous food may be gathered primarily through scavenging.

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